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Spatial Ecology of White-winged Scoters (*Melanitta deglandi*) in Eastern North America: A Multi-year Perspective

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Abstract.—Satellite transmitters were used to describe migration patterns and establish connectivity among breeding and wintering areas for 30 White-winged Scoters (*Melanitta deglandi*) tagged in August 2010 or August 2012 during remigial molt in the St. Lawrence Estuary, Quebec, Canada. Fourteen potential breeding sites were identified in the boreal forest from Quebec to the Northwest Territories, Canada. Most birds molted at marine sites, except for two females that molted close to their breeding areas and a male that molted in interior Manitoba. Most birds remained near their molting location during fall prior to migrating to their wintering area. Individuals tended to use similar fall migration routes from year to year. Most birds (81%) wintered in the Long Island-Nantucket-Cape Cod region along the eastern seaboard of the USA, while only three birds wintered in Canada. Scoters spent almost half the year on wintering areas, and 83% returned within 150 km of the previous year's site. Spring migration patterns depended on breeding status. Breeding birds covered an average of 6,880 km compared to 2,550 km by non-breeding birds during their annual cycle. The St. Lawrence Estuary in Quebec and the Long Island-Nantucket-Cape Cod region (New York state and Massachusetts) were areas particularly important for tagged birds. *Received 29 July 2019, accepted 13 March 2020.*

Key words.—breeding, fall migration, key sites, *Melanitta deglandi*, satellite telemetry, site fidelity, spring migration, staging, White-winged Scoter, wintering

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The delineation of demographically or spatially distinct population units is fundamental to identify the scale at which management actions would be meaningful, for example in designing monitoring surveys, interpreting numerical trends or setting harvest regulations (Sea Duck Joint Venture Management Board 2014; Boyd *et al.* 2015). Furthermore, determining linkages among breeding, wintering, and molting areas is important for identifying, understanding and addressing conservation issues (Swoboda 2007; Boyd *et al.* 2015; Sea Duck Joint Venture Partnership 2015) as evidence is growing of the importance of cross-seasonal effects on the dynamics of waterfowl populations (DeVink *et al.* 2011; Alisauskas and DeVink 2015). Little is known about population delineation of White-winged Scoters (*Melanitta deglandi*) in North America (Brown and Fredrickson 1997; Sea Duck Joint Venture Partnership 2015). While there have been delineation studies for White-winged Scoters

in western North America (e.g., Boyd and Esler 2004; Rosenberg *et al.* 2006; Washington Department of Fish and Wildlife 2014), there has been only one study in eastern North America (Meatley *et al.* 2018).

Breeding locations for eastern North American White-winged Scoters are not well quantified; some confirmed records have been reported from northern Saskatchewan, Ontario, Quebec and Labrador, but the extent of the breeding distribution is unclear (Brown and Fredrickson 1997; Lepage and Savard 2013; R. Alisauskas, Environment and Climate Change Canada [ECCC], unpubl. data). The 2001-2005 atlas of the breeding birds of Ontario only reports probable breeding records in the northern Hudson Bay lowlands, mostly in the more open taiga along Hudson Bay (Ross 2007), while the 1981-1985 atlas provided one confirmed breeding record in this province (Ross 1987). They are scarce in northern Quebec, with a known small concentration breeding

in the lowlands along the northeastern coast of James Bay (Savard and Lamothe 1991; Benoit *et al.* 1991, 1992, 1993), and recently, Meatley *et al.* (2018) documented White-winged Scoter females that bred in Quebec much farther east and inland. In Labrador, only a few pairs have been observed during the breeding season (S. Gilliland, unpubl. data).

Trends in abundance are unknown in eastern North America, as the three species of scoters are not differentiated in traditional fixed-wing airplane surveys (Smith 1995), counts are highly variable from year-to-year, the geographic coverage is likely insufficient, and the timing of surveys is not optimal for this late breeding species (Bowman *et al.* 2015). Coastal surveys along the St. Lawrence River Estuary in Quebec (Falardeau and Savard 2003; Rail and Savard 2003; Lepage and Savard 2013) and coastal Labrador (Lock 1986; S. Gilliland, unpubl. data) have shown that thousands of White-winged Scoters molt and stage there during spring and fall migrations. These aggregations likely consist of birds that breed in eastern North America.

Migration routes of eastern White-winged Scoters were not well identified until recently; Meatley *et al.* (2018) delineated two principal spring routes from the Atlantic coast, along the Canadian Maritimes coast and northwest overland. Earlier studies also reported White-winged Scoters migrating through the Maritimes in spring (Hicklin and Bunker-Popma 2001; Bond *et al.* 2007).

Breeding philopatry of females has been well documented in waterfowl (Anderson *et al.* 1992) and it is thought to be relatively high in many sea ducks (Mallory 2015). There are indications of annual fidelity to wintering areas in some sea ducks, but little is known of yearly fidelity to molting areas and to spring and fall migration routes (Derksen *et al.* 2015; Petersen and Savard 2015; Savard and Petersen 2015).

The objectives of this study were to describe space use of White-winged Scoters in eastern North America throughout their annual cycle, namely: 1) identify potential breeding locations; 2) establish connectivity

among molting, breeding and wintering areas; 3) determine spring and fall migration routes; 4) identify key sites throughout the year; 5) determine annual fidelity to breeding, molting and wintering sites; and 6) determine fidelity to migration routes.

METHODS

Capture Site and Technique

Birds were captured during remigial molt on 7-9 August 2010 and 15-19 August 2012 in the St. Lawrence Estuary near Forestville, Quebec (48° 44' N, 69° 05' W), a known molting area for both Surf (*M. perspicillata*) and White-winged scoters (Savard *et al.* 1999; Rail and Savard 2003). The area is characterized by shallow, sandy, subtidal substrates that harbor high densities of various species of clams, a preferred food of White-winged Scoters (Brown and Fredrickson 1997). The area is also used by scoters during spring and fall migration (Savard *et al.* 1999).

We modified drive-trapping techniques described by Breault and Cheng (1990) to capture flightless molting birds using submerged gill nets (Gilliland *et al.* 2010). Three boats were used to slowly push a flock of molting White-winged scoters towards a submerged gillnet. When near the net, we forced scoters to dive by scaring them with loud noises and by driving the boats close to the flock. Once birds were caught, the net was quickly brought inside one boat to prevent drowning, and birds were untangled and put in individual poultry crates for transport to the veterinarian facility 3.5 km away.

Transmitter Deployment

Nineteen birds (16 males and 3 females) out of 219 captured in 2010, and 17 birds (12 males and 5 females) out of 54 captured in 2012, were selected based on their apparent good condition for surgery. All males were adults (After Second Year, ASY) based on plumage and bill characteristics. In 2010, all females were sub-adults based on plumage (Second Year, SY); in 2012, there was one adult and four SY females based on bursal measurements (Mather and Esler 1999).

Transmitters were implanted by experienced veterinarians into the coelomic cavity of scoters, with an antenna protruding through the back following a technique adapted from Korschgen *et al.* (1996) and Fitzgerald *et al.* (2001). Transmitters implanted in 2010 were from Microwave Telemetry (38-42 g; Microwave Telemetry Inc., Columbia, Maryland). In 2012, 15 transmitters were from Telonics (36-39 g; Telonics Inc., Mesa, Arizona) and two were from Microwave Telemetry. The anesthesia and surgery lasted an average of 59 min and 40 min, respectively. The mean delay between awakening of a bird and its release was 2 hr and 32 min, and the mean duration of captivity at the veterinarian facility was 9 hr 13 min.

Data Acquisition

Transmitters were programmed on a duty-cycle of 2 hr on and 72 hr off. This duty-cycle does not provide much information on fine scale movements or stops of short duration, but extends the life expectancy of the battery up to 3 years to provide insights into fidelity to breeding, molting, and wintering areas, as well as into fidelity to migration routes across years. Transmitter signals were received through the ArgosDirect data delivery system (Collection & Location by Satellite [CLS] America Inc., Lanham, Maryland, USA). All messages received by the satellite were retained. We used detections of Argos location class 3 or 2 to identify site use (i.e., breeding, molting, wintering sites; location class accuracies of < 250 m, 250 to < 500 m, respectively; Collecte Localisation Satellites 2016). Lower quality location classes were used to determine timing of various events. Locations received during the first 60 days following release were removed to reduce potential biases in timing of movements that resulted from effects of surgery. In both capture years, this 60-day gap fell when birds were completing their molt in the St. Lawrence Estuary, then either fall staging onsite (for most of them), or moving to their fall staging area elsewhere; arrival date on wintering site (> 60 days following release) was not different the year of implantation than in subsequent year(s).

Determination of Annual Cycle Periods and Length of Stay

We assigned locations to five general periods of the annual cycle: breeding, molting, wintering, spring migration, and fall migration. We classified a “potential breeding” bird as any bird that settled in an area more than 2 weeks at an inland location between the last week of May and the end of June, while birds not meeting this criterion were classified as “non-breeders”. Any site used for more than 5 weeks (Dickson *et al.* 2012; Viain *et al.* 2014) between early July and late October was considered as a likely molting area. A wintering location was assumed where birds generally ended their fall migration and spent most of their time between November and February. When birds split their time between two distant (> 150 km) areas during the same winter, we considered both locations as wintering areas. We identified the initiation of spring migration as an undertaking of a > 80 km movement between March and May. Similarly, we identified the initiation of fall migration as > 80 km movement from the molting area towards wintering areas. A staging site was defined as an area that birds used for at least two consecutive duty-cycles (> 72 hr).

Data Processing and Statistical Analyses

Data were analyzed using R (R Development Core Team 2018). All data were first read with the R package “Trip” (Sumner 2016). Relocations representing unusually high movement speeds (> 70 km/h) were removed. We created a KMZ file of each bird’s track with each location labeled with date, location class, distance and direction from last location, and each bird’s track was manually annotated.

For each year, we classified the bird’s breeding status as “potential breeding” or “non-breeding”, recorded the arrival and departure dates for each period of the annual cycle (breeding, molting, wintering, and spring and fall migrations), and the date of the last message received. We used the function “Geomean” from the Geosphere package (Hijmans 2016) to estimate mean locations for winter, breeding, and molt. For these estimates, we restricted the data to location class 2 or better and to the best class location per duty-cycle. In a few instances where there were too few locations class 2 or better to calculate the mean, we used the best quality location (location class ≥ 2) to represent the site.

To describe spring and fall migratory patterns across individuals, we used a single spring or fall migration track per individual. When an individual had more than one annual migration, we selected the year with the last complete migration. Each migration track was converted to a line segment pattern, then to a pixel image. We estimated kernel line densities using the Spatstat package (Baddeley *et al.* 2015).

RESULTS

Effective Sample Size

Transmitter performance varied between years, with almost half of the transmitters deployed in 2010 providing locations for more than 2.5 years vs. 2012 when only ~5% of the transmitters lasted more than 2.5 years. Of the 19 scoters tagged in 2010, there was evidence of mortality for four birds and transmitter failure for one bird following surgery. Of the 14 birds/transmitters that survived > 60 days, 12 were tracked through the winter of 2010-11 (9 males and 3 females) and 11 through their spring migration in 2011 (Table 1). Nine of these transmitters (7 males and 2 females) lasted > 2.5 years, yielding information about faithfulness to migration routes and fidelity to breeding, molting and wintering sites. Of the 17 scoters tagged in 2012, one likely died in the weeks following surgery. Of the 16 birds/transmitters that survived > 60 days, 14 were tracked through the winter of 2012-13 (9 males and 5 females) and 12 through their spring migration in 2013. Only one of these transmitters lasted > 2.5 years (Table 1). Our results are therefore based on the 30 birds that survived > 60 days (14 in 2010 and 16 in 2012).

Table 1. Satellite transmitter performance on White-winged Scoters (*Melanitta deglandi*) tagged while molting in the St. Lawrence Estuary near Forestville, Quebec, in August 2010 and August 2012.

	2010		2012	
	No. males	No. females	No. males	No. females
Implanted	16	3	12	5
Lasted >60 days	11	3	11	5
Complete first winter	9	3	9	5
Complete first spring	9	2	8	4
Complete first year	9	2	7	4
Lasted >2.5 years	7	2	1	0

Breeding

We identified 14 potential breeding sites from 11 individuals ranging from Quebec to the Northwest Territories, Canada (Fig. 1). Arrival on the breeding area averaged 4 June \pm 5 days (mean \pm SE; range = 24 May-15 June, n = 16 [includes one female that went back to the same breeding site as the previous year]). Female arrival averaged 3 June \pm 3 days (range = 28 May-5 June, n = 7) and

males 6 June \pm 7 days (range = 24 May-15 June, n = 9). Distance between wintering and breeding areas averaged 3,340 km (range = 1,814-4,996 km). Duration of inland flight (range = 4-30 days) was correlated with distance of the breeding area from the last coastal staging area (R = 0.78; n = 16).

Males stayed on breeding areas an average of 24 \pm 13 days (n = 9), whereas females averaged 60 \pm 12 days (n = 4) when they molted elsewhere, and 109 \pm 21 days (n = 2)

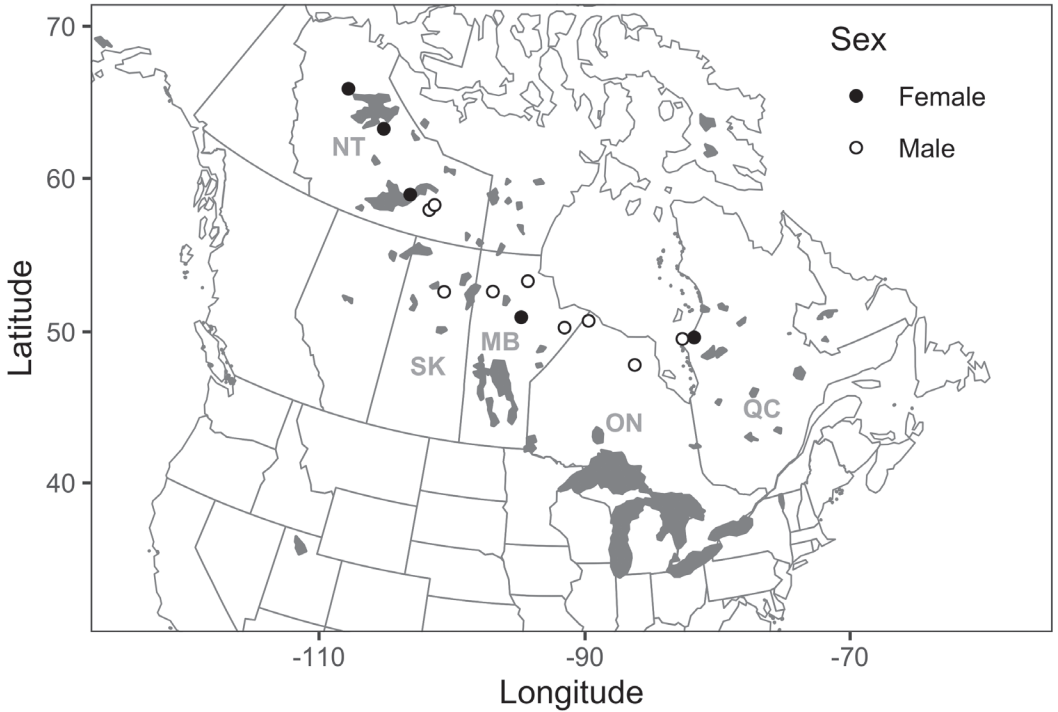


Figure 1. Breeding sites (14 potential sites from 11 individuals) for White-winged Scoters (*Melanitta deglandi*) determined from satellite-tagged birds captured on their molt site in the St. Lawrence Estuary near Forestville, Quebec, in August 2010 and 2012. NT = Northwest Territories; SK = Saskatchewan; MB = Manitoba; ON = Ontario; QC = Quebec.

when they molted near the potential breeding site (Appendix 1). The last day on the breeding areas averaged $28 \text{ June} \pm 11 \text{ days}$ for males ($n = 9$) and $1 \text{ August} \pm 11 \text{ days}$ for females ($n = 4$). The two females that likely molted on their breeding site left much later, 27 September and 4 October, respectively.

Distances covered by breeding birds were much greater than those of non-breeding birds: the round-trip from wintering area to and from breeding area averaged $6,880 \pm 1,816 \text{ km}$ (range = $3,856\text{--}9,393 \text{ km}$; $n = 9$), whereas non-breeding birds, which all went directly to pre-molting coastal areas (see below), averaged only $2,553 \pm 1,073 \text{ km}$ (range = $1,560\text{--}6,164 \text{ km}$; $n = 16$).

Breeding site fidelity. For the two females tracked for 3 years, none went to a breeding area as two-year-old birds the first summer. Instead they spent that summer near their molting site in the St. Lawrence Estuary and went to breeding grounds in subsequent years, with one female using the same breeding site both years, and the other apparently scouting two breeding sites the second sum-

mer and returning to one of these to breed in the third summer (Appendix 1). None of the males that migrated to breeding areas and tracked for at least two complete years ($n = 6$) went to the same breeding location (Appendix 1), and four males tracked for multiple years never went to breeding grounds (Appendix 1).

Molting

Breeding birds. We identified 13 molting locations from 11 birds classified as breeding. A few birds molted on inland waters following their breeding attempt; for example, two females molted near their breeding site and one male molted on an interior lake in Manitoba (Fig. 2). Several other birds classified as breeding went to marine molt sites including: James Bay (three occurrences by males), Hudson Bay (three occurrences by males) and back to the St. Lawrence Estuary (one occurrence by a male and three by females; Fig. 2). Arrival at the molting site was more than a month earlier for presumed

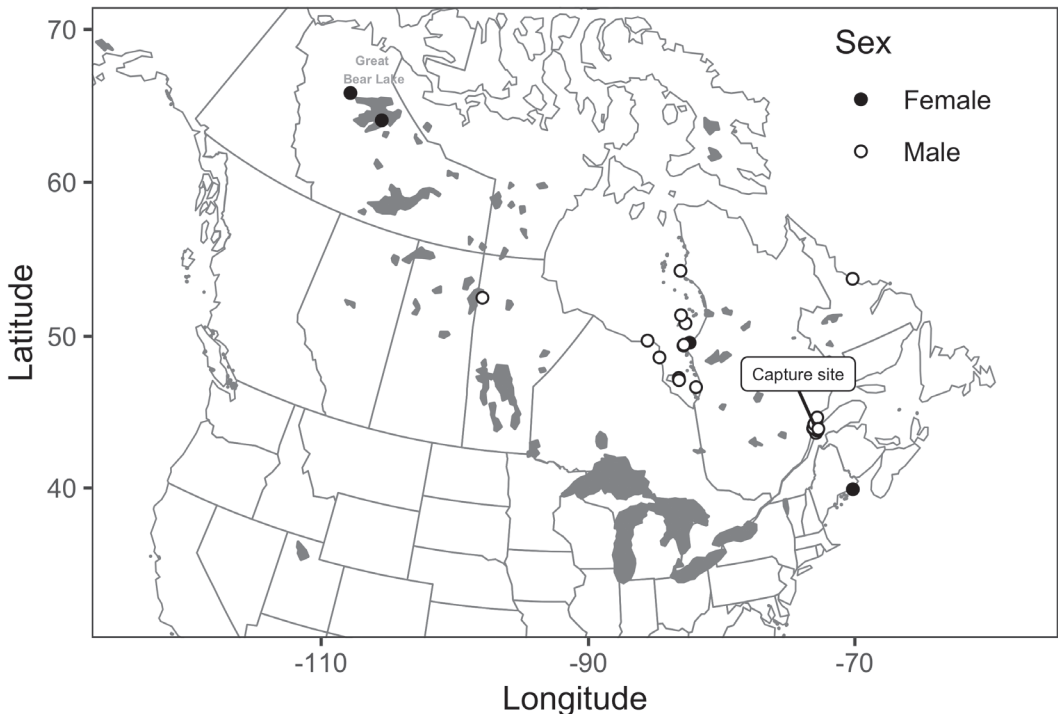


Figure 2. Molting sites for White-winged Scoters (*Melanitta deglandi*) determined from satellite-tagged birds captured on their molt site in the St. Lawrence Estuary near Forestville, Quebec, in August 2010 and 2012.

breeding males (15 July \pm 10 days, $n = 8$) than for breeding females (27 August \pm 14 days, $n = 3$) (Appendix 1).

Distance between breeding sites and the molting location varied from 0 km for the two females that molted on the breeding sites to 3,166 km for a female that bred northwest of the Great Bear Lake, Northwest Territories, and molted in the St. Lawrence Estuary. Excluding the two females that molted on their breeding sites, distance from breeding to molting location averaged 1,403 km (range = 52–3,166 km, $n = 11$).

Non-breeding birds. We identified 21 molting locations from 17 birds that did not go to a breeding area: 11 males (eight once and three twice) and two females molted in the St. Lawrence Estuary, two males in Hudson Bay, one male in James Bay, one male on the Labrador coast, and one female in coastal Maine (Fig. 2). In general, non-breeding birds arrived at their molting area several weeks before becoming flightless, often making local movements before settling at the molting site. For instance, birds that molted in the St. Lawrence Estuary arrived there on 25 May \pm 18 days (range = 21 April–25 June, $n = 16$) and settled at their molting site on 27 June \pm 16 days (range = 30 May–17 July, $n = 16$). The distance between their wintering area and the molt areas ($1,371 \pm 526$ km, $n = 21$) was similar to their return trip from molt to their wintering area ($1,205 \pm 661$ km, $n = 16$) (Appendix 1).

Molting site fidelity. Seventy percent of non-breeding White-winged Scoters ($n = 23$) returned to molt near Forestville in the St. Lawrence Estuary where they were captured. Birds that went to a breeding area were less faithful to their molting area, with only 31% returning to molt in the St. Lawrence ($n = 13$). However, breeding females may be more faithful to their molting location than breeding males; for the five females that went to a potential breeding area, two molted near their breeding area and three returned molting in the St. Lawrence, whereas only one of six males that went to breeding grounds returned to the St. Lawrence to molt.

Fall Migration

Eighteen birds provided 29 fall migrations (Fig. 3b). For half of these migrations, the initial movements following departure from the molting area were < 100 km ($n = 14$; 12 from the St. Lawrence Estuary, one from Hudson Bay and one from the Northwest Territories). The other birds left their molting area and moved to staging areas several hundred kilometers away (seven from the St. Lawrence, five from James-Hudson Bays, and one each from Manitoba, the Northwest Territories and Labrador). For example, several of the birds moved from their molt sites to staging areas in the St. Lawrence Estuary, coastal Labrador, coastal New Brunswick, coastal Prince Edward Island and eastern Lake Ontario (Fig. 3b).

White-winged Scoters spent various amounts of time in the St. Lawrence Estuary, averaging 140 ± 23 days ($n = 8$) for birds that did not migrate to a breeding area, to 70 ± 11 days ($n = 4$) for birds that molted there following breeding, and 39 ± 25 days ($n = 6$) for birds that only staged there in the fall. Birds that molted outside the St. Lawrence but staged there in the fall arrived on average 25 September (range = 11 September–14 October, $n = 6$).

Overall, migration from the three principal fall staging areas (James Bay, St. Lawrence Estuary and coastal Prince Edward Island) to wintering areas was direct (Fig. 3b). Birds that staged in the St. Lawrence Estuary (81%) used a direct overland route via Maine to the Atlantic coast of the USA (Fig. 3b). For these birds, we did not detect other staging sites between their departure from the St. Lawrence and their arrival on the wintering areas. Birds that staged in coastal Prince Edward Island (3 males, 9 movements) had previously molted in St. Lawrence Estuary (Fig. 3b), except for one that molted in Hudson Bay the third year.

Fidelity to fall migration routes. Individual White-winged Scoters tended to use the same fall migration routes from year to year (Appendix 1). Birds that molted and fall staged in the St. Lawrence Estuary flew rapidly to the Atlantic coast of the USA consistently

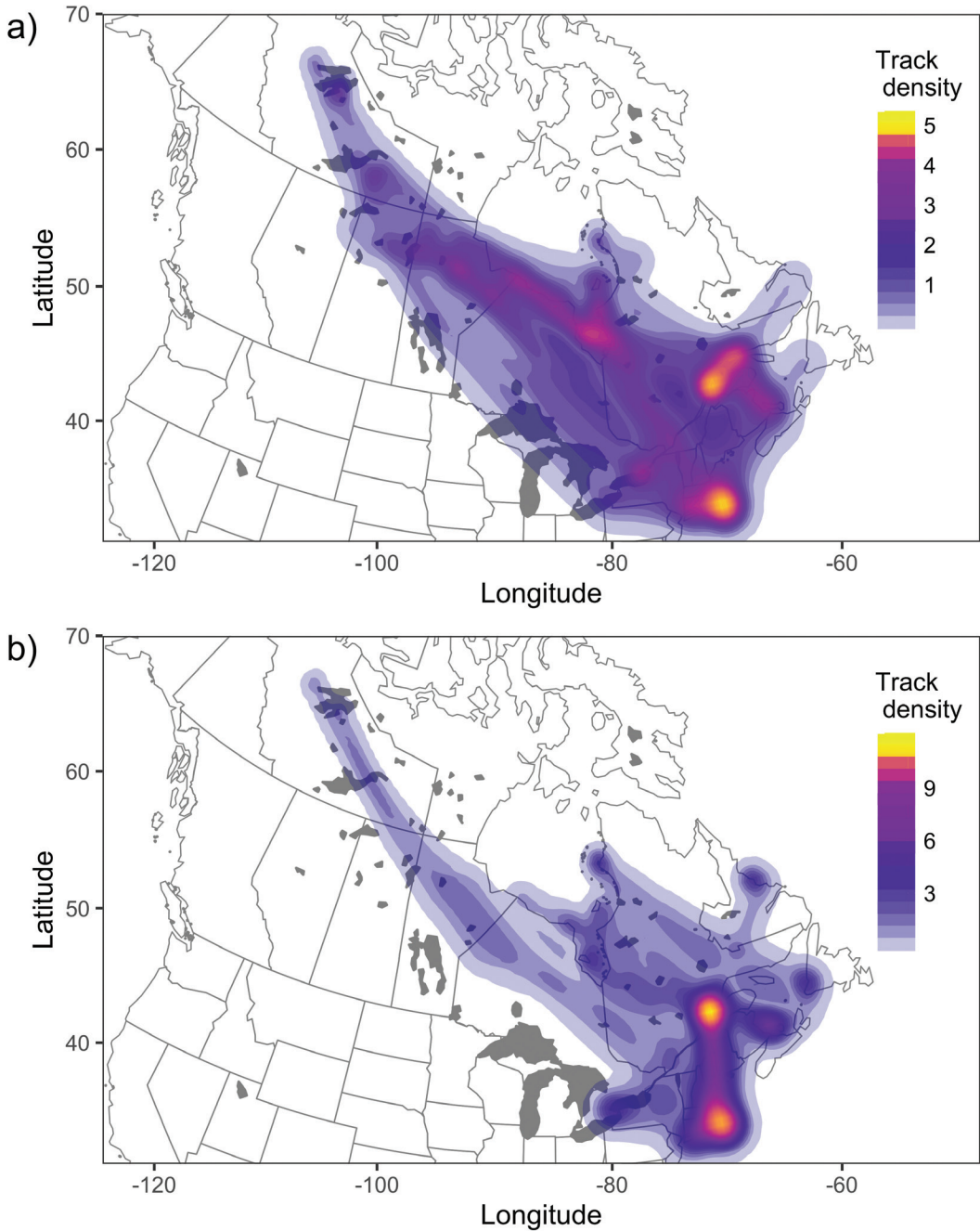


Figure 3. Spring (a) and fall (b) migration patterns for White-winged Scoters (*Melanitta deglandi*) graphically represented as track density (linear kilometers of track per 2,500 km²), estimated from satellite-tagged birds captured on their molt site in the St. Lawrence Estuary near Forestville, Quebec, in August 2010 and 2012.

each year. Only 17% of the scoters tracked over successive fall seasons changed their fall staging area (three out of 18 birds). In general, tagged White-winged Scoters were more faithful to their fall migration route

than to their spring route; given that birds have a variable molting strategy associated with their breeding status, many of them seemed to reincorporate their migration pattern for fall and winter.

Wintering

We documented 53 wintering sites from 26 White-winged Scoters (Fig. 4). Eighty-one percent of the scoters ($n=21$ birds) wintered along the Atlantic coast of the USA in the waters surrounding Long Island (New York state), Nantucket Island and shoals (Massachusetts [MA]), and Cape Cod, MA (Fig. 4). Other wintering locations included the Broad Bay area (near Boston, MA), the vicinity of the Great Boars Head (near Hampton Beach, New Hampshire), St. Mary's Bay (western Nova Scotia), St. George's Bay (near Stephenville, Newfoundland and Labrador), and western Lake Ontario (Ontario; Fig. 4) in Canada. Ninety percent of the birds spent the entire winter in the same area. However, three birds that first wintered around Nantucket shoals later moved to the Long Island coast or the Cape Cod coast, or from one end of Long Island to the other; these scoters spent about half their time at each place over the winter and moved from ~150 to 300 km between sites.

Arrival date on the Atlantic coast of the USA averaged 6 November \pm 16 days in 2010 ($n=9$), 7 November \pm 25 days in 2011 ($n=8$), 6 November \pm 14 days in 2012 ($n=20$), and 29 October \pm 15 days in 2013 ($n=7$) (Appendix 1). Departure from the Atlantic coast wintering areas was dependent on breeding status and location. The average departure date for birds that migrated to a breeding area was 9 April \pm 8 days in 2012 ($n=5$) and 13 April \pm 20 days in 2013 ($n=9$). For non-breeders, the departure date was 3 April \pm 17 days in 2011 ($n=8$), 1 April \pm 21 days in 2012 ($n=2$) and 6 April \pm 20 days in 2013 ($n=3$). The average departure date from their wintering area across years and sites was 12 April \pm 16 days ($n=14$) for birds that went to breed and 3 April \pm 17 days ($n=13$) for non-breeders. However, birds that wintered in the Nantucket area stayed there into May (mean departure date across years: 12 May \pm 5 days, $n=10$) which was about a month later than those wintering elsewhere along the Atlantic coast. Tagged White-winged Scoters wintering along the New England and Long

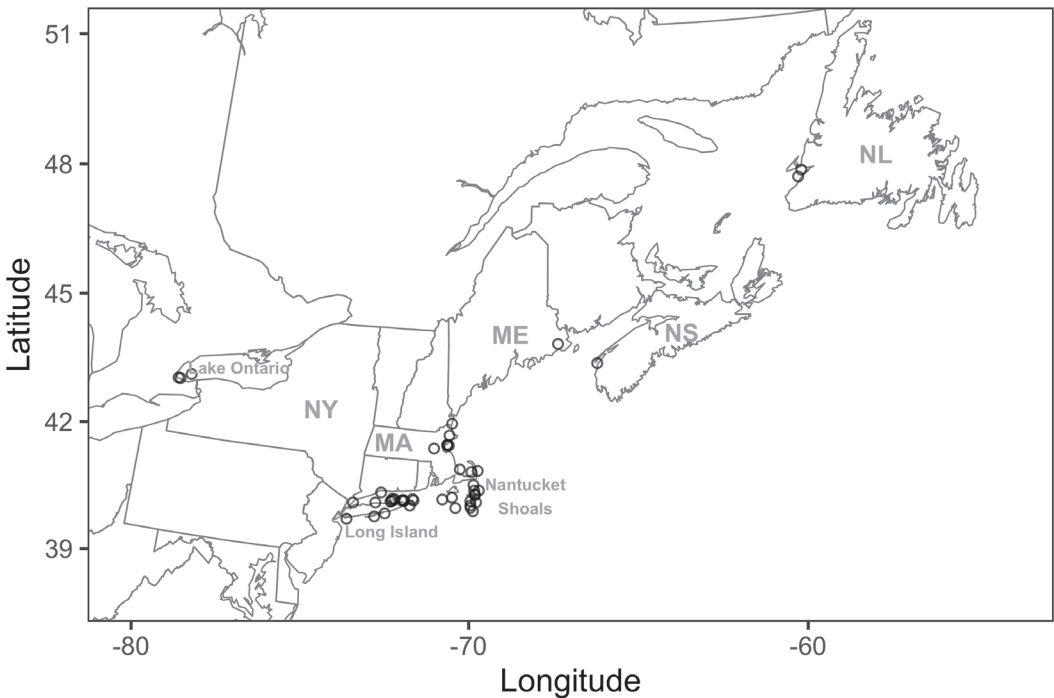


Figure 4. Wintering sites for White-winged Scoters (*Melanitta deglandi*) determined from satellite-tagged birds captured on their molt site in the St. Lawrence Estuary near Forestville, Quebec, in August 2010 and 2012. NY = New York; MA = Massachusetts; ME = Maine; NS = Nova Scotia; NL = Newfoundland and Labrador.

Island coasts spent nearly half a year there (mean = 173 ± 31 days, range = 94–220 days; $n = 37$ cases from 23 birds).

Wintering site fidelity. Eleven birds (61%) returned to the same wintering area (<25 km) used the previous year, four birds (22%) used sites within 150 km of the previous year, and three birds (17%) wintered at sites > 150 km apart from each other. Winter site switching among years occurred between Cape Cod, Nantucket and Long Island areas.

Spring Migration

After departing their wintering areas, birds did not stage on any inland waters except for those birds that used Lake Ontario and Lake Erie. White-winged Scoters used one of three general corridors (Fig. 3a). The primary corridor consisted of an eastbound coastal route along the coast of Maine and up through the Bay of Fundy, across to the Gulf of St. Lawrence in Quebec and into the St. Lawrence Estuary. About half of the non-breeding birds that returned to molt in the St. Lawrence Estuary took this coastal route. While some breeding birds used this route, most took a more direct overland corridor through the USA New England States and over western Quebec and eastern Ontario, or a westbound corridor over the New England States and the State of New York through the eastern Great Lakes, before heading to their breeding areas. As spring migration route and timing was dependent on the breeding status of the bird, we present results separately for both groups of birds.

Breeding birds. We documented 16 spring movements (11 birds) between wintering and breeding areas (Fig. 3a). Most breeding White-winged Scoters initiated spring migration between mid-March and late-April: three birds remained on their wintering locations (Nantucket) until $13 \text{ May} \pm 5$ days before migrating directly to their breeding area; six birds that wintered around Long Island flew ~160 km southeast (mean departure: $2 \text{ April} \pm 17$ days) to Nantucket, where they staged for a few weeks, being last detected there on $14 \text{ May} \pm 3$ days; two

birds staged in the Maritimes and stayed there until 20 May and 27 April, respectively; one remained on its wintering location (Long Island) until 4 May before staging in the St. Lawrence Estuary; and four cases of birds that flew to Lake Ontario or Lake Erie from Long Island to stage there until $19 \text{ May} \pm 3$ days. Six birds had a secondary staging location (St. Lawrence Estuary, Quebec's North Shore, or James Bay) (Appendix 1).

Duration of staging varied between birds ranging from 4 to 58 days, with no particular relation to location. Secondary staging locations were used for a shorter duration (mean = 10 ± 5 days; $n = 6$) than initial staging sites (mean = 31 ± 16 days; $n = 13$). Birds that flew to breeding areas were last located on their coastal staging area on $23 \text{ May} \pm 8$ days in 2012 ($n = 5$), $21 \text{ May} \pm 8$ days in 2013 ($n = 10$) and 17 May in 2014 ($n = 1$), for an average date across years of $22 \text{ May} \pm 8$ days (range = 7 May–2 June; $n = 16$).

Non-breeding birds. Non-breeding White-winged Scoters (19 birds, 25 spring movements), except for birds wintering or staging in Nantucket, initiated their spring migration at the same time as breeding birds. They reached their first staging site around $8 \text{ April} \pm 18$ days ($n = 13$). Contrary to breeding migrants, most non-breeders made frequent stops; although locations used were generally similar to breeders, staging sites in the Maritimes, Quebec's North Shore coast and the St. Lawrence Estuary were used more often by non-breeders (88% of movements vs. 25%, respectively). Non-breeding birds' departure date from the last spring staging area to head to their pre-molting coastal areas was $20 \text{ June} \pm 16$ days in 2011 ($n = 11$), $11 \text{ June} \pm 16$ days in 2012 ($n = 4$) and $19 \text{ June} \pm 12$ days in 2013 ($n = 8$), for an average across years and sites of $18 \text{ June} \pm 14$ days ($n = 23$), about a month later than migrants to breeding areas (Appendix 1).

White-winged Scoters' spring staging sites (for both breeding and non-breeding birds) included the St. Lawrence Estuary and Quebec's North Shore coast ($n = 24$), Chaleur Bay, Bay of Fundy and Gulf coasts of New Brunswick and Prince Edward Island in the Maritimes ($n = 15$), the Nantucket area

($n = 13$), eastern Lake Ontario ($n = 7$), James Bay ($n = 6$), the Massachusetts coast ($n = 3$), the Maine coast ($n = 2$), eastern Hudson Bay ($n = 1$), Lake Erie ($n = 1$) and the Labrador coast ($n = 1$; Fig. 3a). Time spent at spring staging areas in a given year (excluding birds that wintered and spring staged in the Nantucket area) tended to be greater for non-breeding birds (mean = 54 ± 24 days, range = 17–102 days, $n = 23$) than for breeding birds (mean = 35 ± 16 days, range = 16–64 days, $n = 13$).

Fidelity to spring migration routes. We captured multi-year tracking data for 10 birds (eight males, two females). For the two females tracked for 3 years, once they went to a breeding area (on the second and third years), they abandoned their past spring migration route through the St. Lawrence Estuary and used a more direct overland route from Long Island-Nantucket to their western breeding grounds in three of the four movements (Appendix 1). For males that went to presumed breeding grounds, because these destinations differed between years, they changed their spring migration strategy accordingly, usually taking a more direct migration route except for one male that migrated over the State of New York and staged on Lake Ontario in 3 consecutive years before heading to its summer destination (Appendix 1). Three out of four males that never went to breeding grounds for 2 or 3 consecutive years used the same spring migration strategy each year, spring staging in the Maritimes or Lake Ontario before reaching the St. Lawrence Estuary to molt (Appendix 1).

DISCUSSION

This study provided important insights into annual movements, key areas throughout the annual cycle, and fidelity for both male and female White-winged Scoters in eastern North America. The breeding locations of White-winged Scoters tagged in this study suggested the breeding range in eastern North America is larger than described by Brown and Fredrickson (1997). Our re-

sults confirmed affiliation between wintering areas along the Atlantic coast of North America and breeding areas in the Northwest Territories, northern Saskatchewan, Manitoba, Ontario and Quebec (Meatley *et al.* 2018). The breeding areas in Saskatchewan and near Great Bear and Great Slave lakes in the Northwest Territories likely overlap those of birds affiliated with wintering areas on the Pacific coast of North America (S. Boyd, ECCC, unpubl. data). White-winged Scoters breeding at Redberry Lake in northern Saskatchewan winter both on the Pacific (75%) and Atlantic (25%) coasts, based on isotopes (Swoboda 2007) and band recoveries (R. Alisauskas, ECCC, unpubl. data). However, White-winged Scoters banded in Western Canada and Alaska tended to be recovered along the Pacific coast while birds marked in Eastern Canada were recovered along the Atlantic coast (R. Alisauskas, ECCC, unpubl. data). This breeding pattern likely reflects the past isolation of the eastern and western populations during the last glaciation and their subsequent expansion following the retreat of the glaciers (Mengel 1970; Talbot *et al.* 2015). The two scoters presumably breeding in Quebec were on the coastal lowlands of northeastern James Bay, the only known concentration of breeding White-winged Scoters for the province (Benoit *et al.* 1991, 1992, 1993). The two suspected breeding locations in northern Ontario were consistent with past breeding records in that province (Ross 1987, 2007).

Males spent only a few weeks inland whereas females spent at least twice as long and up to 4 months. This exposes females to a different and likely greater predation pressure than males, which likely accounts for the greater proportion of males in most sea duck species (Eadie and Savard 2015). Our results confirmed patterns observed (i.e., breeding site fidelity for females but not for males) in waterfowl in general (Anderson *et al.* 1992) and sea ducks in particular (Phillips and Powell 2006; Takekawa *et al.* 2011; Eadie and Savard 2015; Mallory 2015).

Timing of molt appeared related to breeding status and likely to breeding success for females. Non-breeding males arrived

about a month earlier than presumed breeding males, and breeding females a month later than presumed breeding males. Successful females often abandon their brood before they fledge and depart for their molting location (Brown and Fredrickson 1997). Later molting of females was documented for White-winged Scoters in British Columbia and Alaska (Dickson *et al.* 2012) and in the St. Lawrence Estuary (Lepage and Savard 2007). Similar segregation in molt timing is found in most sea ducks (Viain *et al.* 2014, Savard and Petersen 2015). This segregation of habitat use by sex and reproductive status has important conservation implications as, at a given molting site and time, different segment of the population would be exposed to predators, harvest pressure or other anthropological disturbances.

An unexpected result was the variability of female molting strategies. Some females molted on their breeding area whereas others covered over 2,000 km to reach their previous year molting location in the St. Lawrence Estuary, indicating strong fidelity of some females to molting location. By molting in the St. Lawrence, these females had a shorter fall migration to their wintering area. Meatley *et al.* (2018) documented that 95% of their tagged females that went to breeding grounds ($n = 22$) molted away from it. Factors influencing a female's decision to molt near her breeding site or migrate to a molting location is unknown, but her condition and breeding success likely play a joint role. Savard *et al.* (2007) found that unsuccessful breeding female Surf Scoters stayed on the breeding areas for several weeks before departing for their molting location, while females that raised a brood remained longer. As timing of molt is influenced by hormonal levels (Payne 1972), females with young should molt later than unsuccessful females or females who abandon their young (see Savard *et al.* 1998, 2007 on Surf Scoters).

Fidelity to molting areas has been documented for several species of sea ducks (Flint *et al.* 2000; Phillips and Powell 2006; Savard and Petersen 2015; Meatley *et al.* 2018). Our results indicate that this depends mostly on

breeding status, with most males that never went to breeding grounds molting at the same site all years. All males that migrated to inland breeding areas molted $> 1,000$ km away from their past molting site. In addition, females that successfully raise broods may have fewer options than non-breeding or unsuccessful females. Differential migration in relation to age and breeding status has been documented in other waterfowl (Hohman *et al.* 1992; Oppel *et al.* 2008; Fox *et al.* 2014). Birds do not simply molt at the closest molting area but may travel thousands of kilometers to reach a specific site. Reasons behind these choices have yet to be quantified but likely involve site imprinting to the first molting location, individual condition, and possibly some genetic component (Savard and Petersen 2015; Talbot *et al.* 2015).

Fall migration was difficult to characterize because many birds remained relatively close to their molting location and flew directly from there to their wintering area, as also reported by Meatley *et al.* (2018). Many movements between the St. Lawrence Estuary and the Atlantic coast of the USA—the main corridor we identified—took less than 3 days, and it was possible that birds used a coastal route, but were not detected as the movements occurred in the off cycle of the transmitter (72 hr). However, we detected signals from three birds while migrating over Maine, and a similar route has been described for Common Eiders (*Somateria mollissima*) breeding in the St. Lawrence Estuary and wintering along the Atlantic coast (Gauthier *et al.* 1976).

Over 80% of our tagged birds wintered in the Long Island-Nantucket-Cape Cod region, corroborating Silverman *et al.* (2013) who reported that the Cape Cod and Long Island Sound region was the major wintering area for White-winged Scoters along the USA Atlantic coast. The restricted winter distribution of our tagged White-winged Scoters compared to the one reported by Brown and Fredrickson (1997) suggests some possible relationships between molting and wintering areas, as also mentioned by Meatley *et al.* (2018). The wintering site near Stephen-

ville on the west coast of Newfoundland was unusual as this area is covered with heavy sea ice in most years; the closest wintering White-winged Scoters were reported near the Magdalen Islands, Quebec (Lepage and Savard 2013), by the Bird Islands off Cape Breton, Nova Scotia, across the south coast of Newfoundland, and nearby Saint-Pierre and Miquelon, France (Canadian Wildlife Service, unpubl. data).

Our satellite-tagged White-winged Scoters spent nearly 50% of their annual cycle along the coasts of New England and Long Island, which is consistent with the 52% reported by Meattley *et al.* (2018). This half-year period was also documented for Black Scoters on Southern New England wintering grounds (Loring *et al.* 2014). While most of our White-winged Scoters were sedentary and stayed in the same general area throughout winter, Black Scoters were more often found foraging at more distant sites over a single winter period (Loring *et al.* 2014); this difference could be related to availability of preferred prey (Derksen *et al.* 2015).

Our results suggested that winter site fidelity is high, with > 80% of birds returning to the same general area (< 150 km). Rosenberg *et al.* (2006) observed the same with White-winged Scoters tagged in Prince William Sound, Alaska. This differs from the < 50% site fidelity observed for tagged Atlantic Black Scoters in their Southern New England wintering region (Loring *et al.* 2014). Prey availability is likely a key element to wintering site fidelity as sea ducks use habitats with high prey density and environmental characteristics that minimize the energy costs of foraging (Żydelis and Richman 2015).

Spring migration timing, distance and duration varied between birds, similarly to most sea ducks (Petersen and Savard 2015). Routes depended on breeding status, with suspected breeders generally taking a more direct route to breeding areas, similar to Meattley *et al.* (2018) results. Non-breeding birds migrated at a slower pace than breeding birds, as molting does not have the same time constraints as breeding. Similar variation in spring migration routes were found in Surf Scoters along the Pacific coast (De

La Cruze *et al.* 2009). Petersen (2009) also found that Pacific Common Eiders (*Somateria mollissima v.-nigrum*) wintering in the same location have different spring migration strategies and routes. The movement of most birds from their Long Island wintering site in early spring to the waters just offshore of Nantucket Island suggest that they may be responding to a seasonal prey pulse there, as previously observed for several species of seabirds by Veit *et al.* (2016).

Our results indicated that males may experience different spring migration routes from one year to the next because, when paired, they must follow their mate to her breeding area, and these routes may differ in length by two to three times. To do this, the pair needs to be synchronized in terms of fitness, thus the importance for the female to select a male that will reach her breeding destination. These observations support the mutual-choice hypothesis conferring more importance to female choice in timing of pairing and mate selection (Rodway 2007a, b).

We believe that the St. Lawrence Estuary molt-tagged birds provide a valid representation of the distribution and patterns of movement of White-winged Scoters wintering in eastern North America. First, this site likely supports > 15% of males that winter in the eastern USA and Great Lakes (Lepage and Savard 2013; Silverman *et al.* 2012; Petrie *et al.* 2006). Second, the winter distribution of White-winged Scoters satellite-tagged in Forestville is consistent with the relative abundance of White-winged Scoters estimated through winter aerial surveys (Silverman *et al.* 2012). Third, Meattley *et al.* (2018) concluded that tagged molting White-winged Scoters at the Forestville site provided a broader wintering range than scoters tagged on wintering grounds. However, we acknowledge that more samples, and at other molting sites, are needed to fully confirm this.

Based on our results and those from previous studies (see above), there is an area of sympatry between the breeding ranges of White-winged Scoters that winter in the Atlantic and Pacific coast in the Northwest Territories and Saskatchewan. However, dif-

ferential use of Atlantic vs. Pacific coasts by White-winged Scoters based on telemetry and banding suggests that Eastern and Western populations warrant separate management and monitoring programs. This will facilitate identifying, understanding and addressing conservation issues (including harvest) and key factors limiting population. Indeed, the eastern component appears to be small (in the order of 70,000-80,000 individuals; Petrie *et al.* 2006; Silverman *et al.* 2012) so caution should be used when managing the species. For instance, migrations' timing according to reproductive status may lead to the design of more refined monitoring programs, targeting specific population components. Despite some possible relationships between molting and wintering areas, no clear linkages between specific breeding, molting, and wintering sites in Eastern North America were evident. Meatey *et al.* (2018) also found little evidence of population delineation among eastern White-winged Scoters. We therefore believe that there is no sub-population structuring within the eastern component of White-winged Scoter and recommend managing it globally.

As revealed by our results, some areas are very important for White-winged Scoters and deserve an attentive follow up as some anthropogenic activities (e.g., offshore wind power projects; Loring *et al.* 2014; Meatey *et al.* 2019) could impair the quality of the actual habitat. Many of our satellite-tagged birds used the St. Lawrence Estuary, Quebec, for spring and fall staging as well as molt, with some residing there from the end of May until the end of October. Near-shore sites of high use there include the sector between Pointe à Boisvert and Patte de Lièvre Island, Colombier, and the sector from Les Îlets-Jérémie to the Betsiamites River mouth. Given White-winged Scoters displayed fidelity to wintering areas and spent almost half the year there, the areas of highest use by our birds call for vigilance: this includes the marine water surrounding Martha's Vineyard Island and Nantucket Island, and the Block Island Sound northeast of Long Island.

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APPENDICES

Please find the supplemental content for this article online by clicking on the Supplemental Content tab at: <https://doi.org/10.1675/063.043.0203>

APPENDIX 1

Multi-year movements of 10 White-winged Scoters (*Melanitta deglandi*) with more than 2 years of tracking data and detailed information on arrival and departure dates during spring (from wintering site to molt site) and fall (from molting site to wintering site) migrations for 30 White-winged Scoters captured on their molt site in the St. Lawrence Estuary near Forestville, Quebec, in August 2010 and 2012.